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THE NATURAL HISTORY OF *PAPILIO MACHAON* L. IN BAGDAD

By E. P. Wiltshire

Manuscript received 31st August, 1957

(Read 6th November, 1957)

With 1 Plate and 1 Text-figure

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I. Introduction

Papilio machaon L., a Holarctic butterfly, is widespread and conspicuous in Europe. Despite the long time it has been studied and admired, its interest appears inexhaustible. Some recent articles are mentioned in the references at the end of this paper.

Certain observations on its stages, phenology and distribution in Iraq and other Middle East countries, have already appeared (*see* Peile, 1921, and Wiltshire, 1945, 1957) but a detailed account of the natural history of the colony resident in Bagdad, or indeed of any other colony inhabiting an equally hot climate, has not hitherto been published.

II. Situation and Climate of Bagdad: The Oasis Fauna

Bagdad is the capital of Iraq and lies at only 100 feet (33 m.) above sea-level on lat. 32.30 N., 44.20 E. The climate is dry, subtropical and continental. Text-figure 1 gives the monthly climatic means, the figures being taken from Publication No. 10 of the Ministry of Communications, Bagdad. The same publication states that the yearly average rainfall over 15 years is 140·4 mm., of which virtually none falls in the months of June to September. As a biotope, Bagdad is an oasis in the Mesopotamian mud desert.

For many years the oasis has been ecologically isolated, but this isolation may diminish as irrigation develops. The gardens of Bagdad have always been

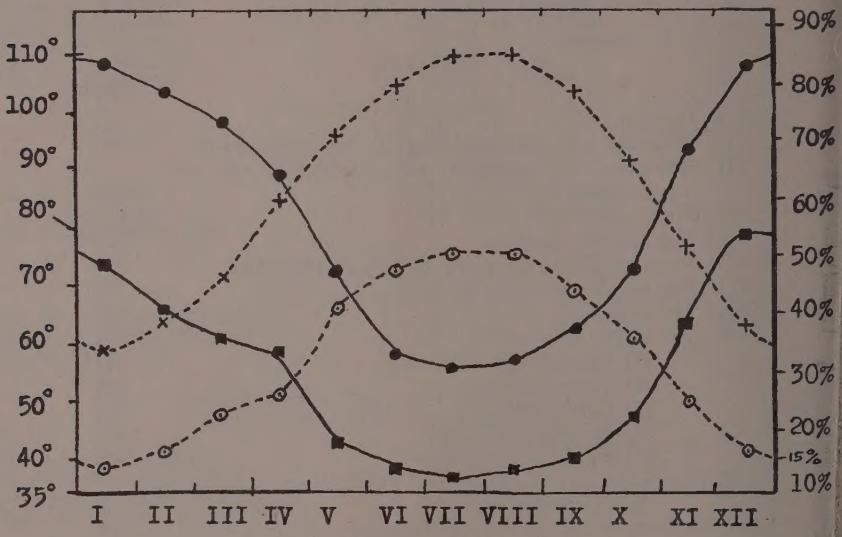

Fig. 1.—Bagdad: monthly climatic means.
On left, temperature (Fahrenheit); monthly mean maximum (×– – – –×) and minimum (⊙– – – –⊙).
On right, humidity; at 03.00 (●———●) and 12.00 (■———■).

irrigated by water lifted from the Tigris which is perennial and wide. Only in the last 30 years have house-gardens, like those in Europe, become numerous. Before World War I the city was a compact mass of houses and alleys; the houses, at the best, had small courtyards where a few trees and herbs were sometimes cultivated. On the river banks, above and below the city, were large date-palm gardens and wheat-fields, and behind these the mud desert. These fields and orchards harbour an isolated oasis biocoenosis, predominantly Palaearctic. This fauna and flora may quite well be derived from the oases of the ancient Babylonian, Seleucian or Abbasid inhabitants of the Mesopotamian plain. The Palaearctic components must originally or more recently have come from the north-east and, in the case of Bagdad, have most probably come down the chain of similar oases fed by the Dyala, a tributary which joins the Tigris shortly below Bagdad. The Dyala oases are similar in crops and

fruits but not in the mode of irrigation. Water is not lifted, but diverted by channel, from the Dyala. However, the last Dyala oasis has for centuries been separated from the Bagdad oasis by an expanse of about 20 miles of mud-desert, liable alternately to floods and desiccation. The arrival of water from the Euphrates on the west bank of the Tigris is, at least as regards modern history, a very recent occurrence; in any case, the Middle Euphrates oasis fauna is isolated from the northern mountains by far greater unirrigated expanses of desert than separate the Tigris from the Zagros mountains to the north-east. There is, therefore, little significance in the irrigation link with the Euphrates for the oasis fauna of the Tigris.

Peile (1921) described a colony of *P. machaon* occurring on a different group of foodplants about 100 km. north of Bagdad on the Zagros foot-hills and along the irrigation canals of the Dyala, where that river flowed through them. It is from this population, therefore, if *machaon* is a fairly recent arrival in Bagdad, that the colony is presumably derived. If, on the other hand, it is of more ancient origin it cannot antedate as an inhabitant the earliest civilisations of the Mesopotamian plain, since it depends, as will be shown, on a cultivated herb for its survival. The first *machaon* colonists, therefore, in the central plain of Iraq, whether ancient or recent, are derived from the Zagros populations.

III. Relations of *P. machaon* subsp. *centralis* Stgr. with Other Subspecies

Current taxonomic practice confirms the above conclusions based on vegetation history, for the Bagdad *machaon* are usually classed as part of subsp. *centralis* Stgr., which inhabits the Zagros mountains, Persia and Central Asia, rather than of the more western subspecies *sphyrus* Hubn., of the Mediterranean basin. The difference between the two is, however, not very great and it is doubtful if the names represent two valid subspecies. In both of them the facies and wing-shape vary seasonally (*see* Section XI (2) below) and there are at least three generations annually. Verity (1947) considered them both as belonging to his " eserge centrale ". He does not mention that ssp. *sphyrus* aestivates in S. Italy but it may be that aestivation has been overlooked. It does, of course, hibernate there. Subspecies *centralis* both aestivates and hibernates over a wide range, for I have observed at Shiraz (5000 feet in the South Zagros, Fars, SW. Persia) that emergence from the pupae of June larvae either takes place quickly or is delayed until autumn after pupal aestivation, exactly as with the summer larvae of Bagdad. It seems likely that in parts of the range of *centralis* where summer is shorter and cooler (*e.g.* Hamadan, 6000 feet, Central Persia) aestivation does not occur, and hibernation is proportionately longer. Probably, too, at the various great heights scattered through the vast range of *centralis* (*e.g.* above 10,000 feet) single-brooded populations, analogous to ssp. *alpica* Vty. in Europe, will be discovered and the adults will presumably exhibit the facies of first generation *centralis* only. Whether *centralis* and *sphyrus* really deserve to be regarded as separate subspecies, and whether any validity can attach to other names given by authors to local populations in the Mediterranean basin and Middle East, may perhaps be settled when biological details, as full as those given below, are available for all these populations. It seems likely that these southern long-flying popula-

tions are multivoltine with a plastic phenology varying with the local climate; races defined in accordance with modern taxonomic practice do not coincide with climate.

IV. Foodplants

This butterfly, as is well known, is oligophagous on certain Umbelliferae and Rutaceae. In Bagdad ovipositing females seem to favour species with a rich oil supply and a strong aroma, and no ova or larvae were ever seen on parsley (*Petroselinum hortense*), though if transferred to this plant the larva appears quite content. All the Bagdad foodplants are cultivated. This justifies the belief that the colony is a purely garden-dwelling one. Of the three plants selected by females, the first of those listed below is the only one used by all generations. Foodplants sited in sunny places are naturally selected in preference to those in the shade, as the female oviposits under the stimulus of direct sunlight.

(1) Rue (*Ruta graveolens*)

For reasons[1] associated with herbalism and perhaps also certain magical traditions inherited from the remote past, many houses in Bagdad cultivate a bush or two of this herb, either in pots or flower-beds. The herb is perennially green and soon develops a woody stock. It is usually grown by planting small slips; such plants are almost invariably found by females of the butterfly as soon as they attain a height of about nine inches; its gay caterpillars are therefore familiar to all observant persons. The herb's strong aroma, due to ethereal oil in its leaves, probably helps to attract the females. If watered a plant grows in two years into a large shady bush about 1 metre high; its leaves provide the principal pabulum of the larva. Though widely distributed in the city and its suburbs, the herb is by no means common; it is indispensable to the butterfly colony which could not survive in Bagdad without it. It is the principal foodplant.

(2) Dill (*Anethum graveolens*)

This herb is used for flavouring food and is planted, by seed, in vegetable gardens in spring. It seeds in May and is usually up-rooted shortly after to make way for summer vegetables. For the rest of the year it is sold for flavouring in a dry state and the seeds are kept until the next spring. But a few plants may remain on the borders of garden-plots until autumn if in a shady and fairly well watered spot. Not being available on a wide scale in the autumn, it can only be regarded as a supplementary foodplant for the first and second generations. It is undoubtedly attractive to the butterfly; the flowers rather than the leaves are eaten. It provides no shade, the leaves being thin and linear.

[1] In a modern Arabic medical encyclopaedia (1937, Shaikh Daoud adh-Dharir al Antaki, *Al Jiz' al Awwal min Tadhkurah Ula al Albab wal Jami' lil 'Ajab al 'Ajab*, Uthman Khalifah at the Ottoman-Egyptian Press, Kafr az Zahari) Rue (Arabic: Sadhab) would appear to be almost a panacea. By oral tradition in Bagdad it is the chief ingredient in a standard sedative and remedy for hysteria. In certain circles its odour is also considered a protection against the evil eye.

(3) Lime and orange trees (*Citrus* sp.)

These trees are commonly grown in both date and house gardens in and around Bagdad. If the butterfly could adapt itself to using them as a usual foodplant it would be more common; but they only exceptionally attract ovipositing females. The few cases observed have been in April, when the butterfly has been successfully reared on an exclusive diet of *Citrus* leaves. Despite their abundance, these trees, therefore, are not a basis for the colony's survival.

V. The Habitat Observed

The general biotope, that of an oasis in an extreme desert climate, has been described in Section II. The observations detailed below were made in my garden in West Bagdad between March 1953 and May 1957. They have been compared with and supplemented by less detailed and continuous observations made by friends or myself in other Bagdad gardens in 1935–37 and 1952–57.

In the winter of 1952–53 four or five slips of rue were planted surrounding a small grass plot. In March, 1953, females of *P. machaon* found and oviposited on these plants; since then I have observed all stages of the butterfly continuously in this habitat, except during my absences in June to October, 1953, and June to October, 1955. The colony in my garden was thus observed almost daily for two periods of 21 and 18 months.

The plot was close to the south side of the house and the north wall of the garden. The garden itself was, except for four date palms, newly made when the house was built in 1951. Vegetation adjacent to the grass plot and rue bushes consisted of a larger lawn, myrtle hedges, vines, oleander, *Canna*, other flowers, creepers, orange-trees and palm trees. The nearest palm tree was seven yards away. A certain amount of afternoon shade was provided by these trees and other palms outside the garden. The adjacent ground outside was, except for other palms, bare trodden mud, and the nearest habitats with a food plant of the butterfly were more than a quarter of a mile away.

By 1957 the grass plot was bordered, and indeed half over-laid, by eight rue bushes, two or three of which were dense, many-branched and about a cubic metre in size. About ten other slips of rue, planted elsewhere in the garden in 1955, had also by 1957 developed into fair-sized bushes; they were mostly in rather shady places.

In the spring of 1955, and again in the spring of 1957, a small plot of dill (*Anethum graveolens*) was planted at the other end of the garden among kitchen herbs and vegetables. This plot received no shade. The dill, which is a quick-growing annual of slight stature, immediately attracted *machaon* females, and larvae of the first and second, but not the third or later generations, were found on it. The micro-climate of the dill-plot differed from that of the rue-plot and these differences were reflected in different coloration of contemporary larvae on the two plots, as will be described later under Section IX(1).

In addition to the observations of the butterfly in all stages wild in the garden, larvae in their last instar were repeatedly brought indoors and allowed to complete their growth in gauze and wood cages. Indoors they lacked all sunlight, and were subject to lower and somewhat less variable temperatures; but except for one individual (B in Table I) pupal periods and emergence dates

of these captives did not differ, as far as could be seen, from those living wild in the garden.

VI. Density of the General Population and Mobility

The butterfly is an active flier and, without being a true migrant, is capable of flights of several miles in search of fresh habitats. The Bagdad oasis which is the biotope of the colony is at least 50 square miles in area, and contains many scattered habitats similar to my garden. There is no reason to suppose that the population needs reinforcements from beyond the surrounding desert. The adult is not stenoecous in habit. It is seldom seen commonly in any one garden on the wing. On emerging both males and virgin females were invariably seen to fly out of the garden as soon as they were able and the sun came out; they usually first soared to some height. Many ova were laid on the dill or rue bushes without my ever seeing the females; they obviously visited the garden to deposit a few ova in the course of active flights about the city and its suburbs. At most two or three individuals might be seen flying on a single day in the garden. Single individuals would sometimes be seen flying strongly in the more residential parts of the city. The density of the adult population cannot therefore compare with that of some other butterflies in Bagdad, e.g. *Pieris rapae*, which is on the wing more continuously and in greater strength, doubtless partly because of its migratory tendencies. An increased density of foodplant in 1955 did not result in an increased density of adult population; this was partly because greater concentrations of larvae led to increased predation, while isolated larvae tended to be more immune to enemies; it was also partly due to the roving habits of the adult, just described.

VII. The Weather and the Life-cycle

In contrast to the two migrant and resident butterflies *Pieris rapae* and *Cosmolyce boeticus*, which have been observed in every month of the year in Bagdad, though not in equal numbers in each, *P. machaon*, which is not a migrant, shows more sensitivity to climate and weather. The phenology is multivoltine but interrupted by hibernation and aestivation. These regular diapauses adapt the insect to the climate. The weather, however, causes the phenology to vary somewhat from year to year.

The observations made during four years are summarised below month by month, preceded by a note on the different weather during the four winters. Less variation between different years was observed in larval development during the latter part of the year, and therefore details for each year are only given for the first six months.

Winter 1953–54 was normally cold and approximated to the mean shown in text-figure 1. Winter 1954–55 was abnormally mild. Winter 1955–56 was cold early and followed by a mild spring, which became wet and cool as summer drew on.

Larval hibernation, which is exceptional and was in no case observed to begin before January, was noted during the first and fourth winters. Pupal hibernation, which is normal and begins in autumn, was observed in all four winters. In 1956–57 the early cold seemed to cause a greater retardment in growth of the larva and consequently a later larval diapause.

TABLE I.—*Dates of individual* P. machaon centralis *Stgr. captive larvae and pupae, showing seasonal variation in prepupal and pupal periods*

Individual	Stopped feeding	Suspended	Pupated	Hatched 1955	Prepupal period (length in days)	Pupal period (length in days)
				First generation		
A . .	28.x	29.x	30.x	1.iii	2	120
B . .	4.xi	5.xi	6.xi	10.i	2	77
C . .	16.xi	17.xi	19.xi	26.ii	3	68
D . .	16.xi	17.xi	19.xi	2.iv	3	134
E . .	6.xii	7.xii	10.xii	20.ii	4	72
F . .	4.xii	5.xii	8.xii	16.ii	4	70
G . .	27.xii	28.xii	30.xii	13.ii	3	45
H . .	29.xii	30.xii	2.i	19.ii	4	48
J . .	14.i	15.i	18.i	3.ii	4	16
K . .	26.i	30.i	2.ii	16.iii	7	42
				Second generation		
L . .	27.iii	28.iii	30.iii	12.iv	3	13
M . .	? (FP)	?	(?) 6.iv	18.iv	?	(?) 12
P 1–5 . .	?	?	15–17.iv	26–28.iv	?	11
				Third generation		
Q . .	13.v	13.v	14.v	PD	1	.
R . .	14.v	15.v	16.v	(TE) 6.vii	2	50
S . .	18.v	19.v	19.v	UD	1	.
T . .	19.v	19.v	21.v	(TE) 1.vii	2	40
U . .	20.v	22.v	22.v	(TE) 4.vii	2	42
				1954		
				Third generation		
4V . .	?	?	19.vi	27.ix	?	100
4W 1 and 2 .	?	?	5, 6—ix	12.ix	?	6, 7
				1957		
				First generation		
VV . .	22.x	23.x	25.x	17.iv	3	173
WW . .	23.x	24.x	25.x	21.iv	2	177
XX . .	27.x	28.x	30.x	17.iv	3	168
Z1 . .	9.xii	10.xii	13.xii	USA	4	.
Z2 . .	10.xii	11.xii	16.xii	USA	6	.
Z3 . .	8.xii	9.xii	12.xii	USA	4	.
Z4 . .	9.xii	10.xii	13.xii	USA	4	.
Z5 . .	16.xii	17.xii	22.xii	USA	6	.
Z6 . .	17.xii	19.xii	23.xii	USA	6	.
Z7 . .	22.xii	26.xii	30.xii	USA	8	.
Z8 . .	26.xii	28.xii	31.xii	USA	5	.
YY . .	20.i	f25.i	29.i	ID	9	.
ZZ . .	9.ii	11.ii	15.ii	15.iii	6	28

Explanation of abbreviations:

f: fell from perch.

FP: found as pupa.

ID: died through injury.

PD: died, parasitised.

TE: transferred to England as pupa (left Bagdad 14.vi, arrived England 23.vi).

USA: these pupae were despatched by post to America and dates of hatching are not known.

UD: died from unknown cause.

?: exact date not noted.

January

No adults were ever seen wild in this month. Full grown larvae with a melanistic tendency were observed on the rue in all four years.

1954 : Some larvae pupated ; all disappeared by 29.i, including hibernators whose hiding place was not discovered.

1955, 1956 : All larvae pupated during this month ; the emergence of one adult (B in Table I) was premature and probably due to keeping the pupa in a room occasionally warmed by a stove.

1957 : About 12 larvae, mostly f. *nigricans*, were observed on nine different rue bushes. Some began pupation-walks early in the month but others did not reach the last instar until the middle of the month ; towards the end some were observed in a torpid state low down on the bushes and one of these, a few days later, was on the surface of the ground ; this one, however, when taken indoors into an unheated room, suspended and pupated but fell and fatally injured itself (YY in Table I) ; fewer larvae were visible at the end of the month.

February

In only two of the four years were larvae seen during this month. Adults were seen in some years.

1954 : No larvae were seen until the end of the month when several melanistic hibernators reappeared and again began feeding.

1955, 1956 : Just as fruit trees blossomed three weeks earlier than normal, adults of *machaon* likewise began to hatch in the middle of the month ; no larva was visible.

1957 : The remaining larvae were feeding less frequently and some descended to low points on stems ; one taken indoors into an unheated room pupated and emerged during the next month (ZZ in Table I) ; another was observed to remain one day on the ground before remounting the stem ; these torpid larvae appeared shrunken but prepupal defecation was observed in some cases, when fairly prompt pupation rather than hibernation presumably ensued ; after the middle of the month no more were to be seen, but later observation showed that at least four were hibernating ; their place of hiding, despite some search, could not be found.

March

In two years no larva was seen during this month ; adults were seen in all four years.

1954 : The larvae which had resumed feeding after hibernation left the rue and pupated early in the month ; adults were observed flying and ovipositing during the second half ; adults emerged from captive pupae formed between 4 and 17.i.54 or earlier.

1955 : Larvae from ova laid on dill by first generation adults in February fed rapidly and pupated at the end of iii.55.

1957 : Despite moist warm weather no larva was seen and the diapause of the four hibernators was unaffected ; a captive pupa produced an adult after a pupal period of only 28 days in an unheated room.

April

Larvae were observed in all four years : adults also were seen during this month each year but in one these belonged to an early second generation.

1954 : Some larvae from ova laid by March parents were full grown at the end of the month ; adults, doubtless late individuals of the first generation, were seen flying on various dates.

1955 : The last captive winter pupae hatched on 2.iv.55 and the first of the second generation (L in Table I) on 12.iv.55.

1956 : There was a remarkable cold spell at the beginning of the month.

1957 : On the first of the month the hibernators reappeared on the rue and after three to four days' feeding disappeared to pupate ; larval diapause was thus later in 1957 than in 1954 and this may probably be attributed to the unusually early cold of the winter of 1956–57, which caused a slower larval growth in mid-winter ; it seems to prove also that the larva cannot hibernate before the last instar ; on 3.iv.57 the first ovum was observed, laid on dill ; this year no ovum was seen laid on rue, presumably because the ovipositing female chanced to visit the garden at an hour when only the dill was sunlit ; larvae from these dill ova were full grown and disappeared to pupate by the end of the month ; from captive pupae formed in October, 1956, adults emerged after diapause of 167–177 days, a month later than one adult from a pupa formed early in 1957.

May

In one year pupae began their summer diapause and adults of both the second and third (partial) broods were on the wing in this month, separated by a distinct interval ; but in other years development was not so forward and a third generation had not yet appeared ; in most years larvae of different stages of growth were observed feeding together during the month.

1954 : Larvae of all sizes were seen feeding on rue throughout the month ; second generation adults emerged on 9.v.54 and wild adults were seen flying at later dates.

1955 : Some second generation larvae pupated in the middle of the month ; the last adult of this generation was seen flying on 1.v.55 and after an interval of three weeks third generation adults were observed on the wing ; on dill, larval form *albicans* in final instar appeared in the middle of the month ; on rue normally coloured larvae began to feed less high on the plant ; the less leafy dill provides no shade comparable with that of the rue foliage ; captive pupae of the second generation began to develop quickly or, alternatively, began a diapause. To judge from third generation wild adults the quick developing pupae hatched after nine days but unfortunately those in captivity died, after wing-colouring showed, as explained in Section XII ; from one a dipterous parasite emerged.

June

In normal years pupal diapause presumably begins this month ; in only one year were larvae observed to develop successfully throughout the month ; predation was intense, details being given in Section XII ; dill normally ceases to be a possible foodplant after this month every year as it is uprooted and dried ; nor has *Citrus* foliage been observed as a foodplant in the latter half of any year, though available.

1954 : During the first half of the month, larvae of all sizes were seen feeding ; during the second half, only very small ones were seen ; the absence of larger

larvae after 20.vi.54 was due to their leaving the foodplant either to pupate or aestivate, it being impossible to observe closely each larva when this happened ; the place of aestivation was not discovered ; pupae formed in capitivity in the middle of the month began a diapause ; all larvae preferred the shadier parts of the rue bushes ; adults were still seen flying until the end of the month, having presumably emerged from non-aestivating pupae, a partial third generation.

1955 : Larvae from ova laid on rue by third generation females during late May showed a tendency, even in early instars, to whiter colouring ; they disappeared after attaining the third instar through predation rather than aestivation ; a medium-sized orange wasp, *Polistes hebraeus* F., was seen carrying off small larvae or searching amongst rue foliage ; the mangled remains of some larvae were also seen on rue leaves ; possibly a spider was responsible in such cases ; smaller larvae hatching from ova a week or two later (*i.e.* during the first week of the month) were similarly exterminated and disappeared.

July

In one year only were larvae noted in July, but in 1953, 1955 and 1957 I was away from Bagdad ; surviving larvae presumably begin a larval diapause in this month, and so do pupae, if formed.

1954 : During the first part of the month half grown or full grown larvae were seen on rue, feeding ; they were more whitish than usual (f. *albicans*) ; during the second half, none was seen ; some of these larvae were proved by later observation to begin aestivating but direct observation was not possible, and it was not known in some cases whether a larva disappeared to pupate or aestivate ; adults were occasionally seen on the wing but not later than 13.vii.54; no fresh ova were deposited.

August

The aestivating pupal stage in captivity was the only one seen throughout this month in 1954 and 1956 ; I was away from Bagdad for the same three years as for July.

September

Larvae and adults were to be seen during this month, though the adults were only so observed in one year ; I was away from Bagdad as for July and August.

1954 : Aestivating larvae, full grown and of f. *albicans*, reappeared and resumed feeding for three to eight days, then pupated high up in the rue foliage where they had been feeding ; the fact that no smaller larva reappeared indicates that larvae cannot aestivate before the last instar ; from these pupae adults hatched in six to seven days ; the captive aestivating pupa formed on 19.vi.54 hatched on 27.ix.54 ; on 28.ix.54 ova were noted on the rue ; they hatched five days later.

October

This month is invariably one of great larval and adult activity.

Most of the young larvae hatching in September or early October, and seen high up on the rue foliage, disappeared or were found mangled by predators (*see* Section XII) ; later in the month, however, fresh small larvae in similar situations escaped this fate and fed successfully ; probably a few earlier larvae,

which by chance have been feeding low down and hidden, escape the fate of their contemporaries, as two larvae were noted to pupate at the end of the month, a time when many small larvae were also seen ; adults were seen flying throughout the month.

November

Adults and larvae were both seen in this month every year, but the adults only during the first half.

Ova continued to be laid during the early part of the month but not after the 14th ; they hatched after less than a week ; the latest date on which a butterfly was noted flying in any year in Bagdad was 17.xi.1937 ; one would, therefore, have expected a partial hatch of adults in November from captive pupae formed between 20th and 30th October, but in fact they all started a hibernatory diapause ; breeding therefore failed to establish that two successive broods can occur after the summer diapause, but the adult phenology, as observed wild, suggests that this does occur ; larvae of all sizes were seen feeding on rue throughout the month, some pupating before the end.

December

No adult was ever seen in this month ; a tendency to melanism was noted in larvae on rue in this month every year, though only in two years was it cold ; larvae tended to be of different sizes and this must be attributed both to different oviposition dates (in the previous month) and to different individual rates of growth ; growth rates vary more in cold weather than in hot ; the whole month was unusually cold in 1956 ; in 1953 it became normally cold in the second half ; in 1954 and 1955 it remained mild and permitted a faster growth rate ; all larvae reaching the last instar in this month pupated ; larval diapause was in no case observed or thought to begin in this month.

VIII. The Ovum

This stage was invariably short and incapable of diapause. Eggs hatched after five to seven days.

IX. The Larva

(1) *Coloration in last Instar*

In Bagdad climatic and microclimatic conditions seemed to produced uniform results in contemporary larvae, both season and foodplant-structure having their characteristically-coloured type. The larvae vary from a melanistic form (f. *nigricans* de Frionnet, 1906) through the normal green and black form, to an albinistic form which I have recently named *albicans* (Wiltshire, 1957).[2] In Bagdad *nigricans* appears only in winter and *albicans* only in summer.

Larval form *nigricans* (Plate I, figs. 4 and 5) has the usual green ground colour almost completely obscured by black. This results from the widening of the black transverse bands of which there are two per somite, one across the middle and the second in the intersegmental joint. The orange spots are never diminished or obscured by the black suffusion, which only affects the green areas. In the extreme form (fig. 5) the black bands coalesce so as to leave no green bands on the central somites (4–9), where only a few green

[2] The description given here is however more detailed than in that book.

sublateral and ventral dapplings remain. Form *nigricans* is seen from November to February.

The normal larval form is that in which the green and black bands are equally balanced ; the orange spots, placed on the middle transverse band, are enclosed with black. This form occurs in October–November and March–April, and rarely in other months.

An intermediate between the normal form and f. *albicans* has the black bands slightly reduced so that the orange spots are not surrounded by black but touch the green areas on one side directly. The green colour is retained in this form, which occurs in Bagdad in April on dill, and in May on rue.

The larval form *albicans* (Pl. I, fig. 3) has the black markings further reduced and almost absent from the central somites (s. 4–9) ; the ground colour becomes whitish instead of green. The feet are whitish, lacking black pigmentation. This form occurs in Bagdad in exposed situations, *e.g.* on dill, as early as May and on rue in July and September.

The form *nigricans* Frionnet was observed equally on bushes where there were several larvae and those on which there was only one. Overcrowding, therefore, cannot be a factor in causing it. It is clear that melanism in larvae is not of uniform origin, and that its occurrence in *machaon* is not due to the same causes as have been observed in other species and recorded in Faure (1943) and Long (1953). Far from being due to population density, in Bagdad the variable larval coloration is evidently a direct reaction to the climate, though there is perhaps doubt as to whether this operates directly on the larva or indirectly through the foodplant. Extreme heat and brilliant uninterrupted sunlight produce *albicans* ; the reverse, *nigricans*. Intermediate conditions produce intermediate forms.

Other populations of subsp. *centralis* do not show this phenomenon so strikingly. For instance, at Shiraz (referred to in Section III) f. *albicans* was never seen in gardens though the intermediate form between it and the green form was seen there, accompanied by f. *nigricans* in early summer. The two, strikingly different, larvae were contemporaries and on the same foodplant ; they were probably from a single parent ; it seems unlikely that they had been exposed to different micro-climates. In Bagdad f. *nigricans* never appeared in summer ; but though prevalent in winter months it was occasionally accompanied by a more normal green form larva. It seems likely therefore that the Shiraz population has a slightly different genetic make-up, resulting in a greater degree of larval polymorphism and a less clear-cut reaction to climatic influences.

In Section XI (2) the possible linkage of larval and adult melanism is discussed.

The extreme forms *nigricans* and *albicans* are here treated as forms of the last instar coloration only. It is well-known that the freshly-hatched larva is almost entirely black. In Bagdad the tendency to the one or the other form can often be detected as early as the third instar.

(2) *Larval Diapause*

The place of diapause was unfortunately not observed ; what was observed was the disappearance, and reappearance after an interval, of the full grown

larva. Presumably diapause was spent in the ground or low down on the foodplant stems or amongst thick foliage or litter.

Only the last instar was capable of diapause. Larvae in this instar aestivated in July–August and hibernated in February or March. Larvae of this instar, reaching maturity before certain critical dates, pupated without diapause.

For hibernation, the critical date varies between late January and early February, as is evident from the respective 1954 and 1957 observations given in Section VII. Once a true diapause has set in, the 1957 observations suggest that mild weather cannot break it; but in two other years, milder weather earlier in the winter resulted in no larvae hibernating (*see K* in Table I). For aestivation less evidence is available, owing to my summer absences from Bagdad, but in 1954 the critical date was mid-July. In 1955, which was an early year, although pupal aestivation began earlier than in 1954, no case of larval aestivation was observed. Perhaps larval diapause occurs only when abnormally late larvae are suddenly confronted with the climatic extreme and it then takes place at the earliest stage physiologically possible, *i.e.* the final larval instar; in some, perhaps most, years there are no late summer larvae, just as in some (two out of the four observed) there were no such late winter ones.

It must be admitted that it was difficult in all cases to observe whether a larva disappeared from the foodplant in order to undergo diapause or to pupate, or because it was a victim of predation. It is for this reason impossible to be certain that larval diapause does not begin before the suggested critical dates. No captive larvae underwent diapause, though in February, 1957, larvae, which it was hoped were beginning to hibernate, were taken indoors for observation, but they proceeded to pupate. Doubtless larval diapause is rather exceptional in *machaon* and perhaps 90 per cent. of larvae pupate with no true suspension of biological processes; in the remaining 10 per cent. diapause occurs and the cause may well be genetic, as the individual ZZ (in Table I), which pupated when taken into captivity, was probably not more advanced than the four hibernators of the same year which reappeared in early April, and had been subject to identical conditions in the wild. The reappearance of larvae after disappearance has been assumed to prove that diapause has taken place, but its length can only be guessed from the general disappearance of larvae, in default of observation of individuals in that state. Larval diapause was thus presumed to last about 60 days in midsummer and 30 (1954) or 40 (1957) in winter.

Larvae that had aestivated or hibernated required to eat for a short period before pupating. The resulting pupae had shorter periods before hatching than those formed by larvae which had not undergone diapause.

(3) *Larval Period*

In the spring and early summer the usual larval period from hatching from the egg to pupation was about 30 days. Doubtless this varies, but it was not possible to ascertain the extremes of shortness or length of the period. Perhaps the winter larvae normally take as much as 60 days without hibernation. When diapause occurs, as described above, 60 (for aestivation) or 30 or 40 days (for hibernation) must be added to the larval period.

In 1955 the larval broods were more distinct than in 1954 and the periods could be more exactly observed. Three successive generations before midsummer were observed in 1955. There was no overlapping. All contemporary larvae appeared to grow at about the same speed. No case was observed of a brood dividing into a quick- and a slow-growing group, as has been observed in some other species of Lepidoptera. As the result of my 1955 observations I formed the definite impression that the rate of larval growth during the first half of the year was uniform in all individuals of a brood and only varied during the year according to the month, *i.e.* temperature. The presence together, therefore, of larvae of various sizes in these months as noted in 1954, which is regarded as a normal year, appears to be due principally to different dates of oviposition ; these in turn are the consequence of the variability of the pupal period when in diapause (*see* Section X(2)). However, during the winter 1956–57, which was cold at first and mild later, rates of growth did vary individually, perhaps because of exceptional weather conditions. It may well be, too, that cold causes greater variation in rate of growth than heat.

(4) *Feeding Behaviour*

Usually the larvae fed only by day and by night rested on the foodplant in the place where they had been feeding ; but exceptionally an individual was seen feeding at night, both in summer and winter.

The larvae did not move much. Indeed it appeared that they moved the minimum distance necessary to reach food after consuming the leaves immediately to hand so that they did not interfere with one another, even when there were a number on a single plant.

In the summer the larvae preferred to rest and feed less exposed to the sun, taking refuge amid the abundant, aromatic green foliage of the rue bushes as far as possible. In the spring, autumn and winter they exposed themselves more on the foodplant, with the exception of those observed in January and February 1957, which became torpid low down on the bushes.

With regard to the part of the plant eaten, it was noted that (*a*) of rue, flowers and leaves but not seeds were eaten, the leaves being preferred ; (*b*) of dill, the flowers and seeds were eaten almost exclusively, since the leaves were so thread-like that they would provide little food ; and (*c*) of *citrus*, the leaves only were eaten. On rue and citrus, the young fresh leaves were preferred.

(5) *Pre-pupal Behaviour*

The spinning of the pupation carpet and pupal sling by the larva has been dealt with in many standard works, and need not be described again here. The places chosen for pupation by the wild larva and the prepupal wandering have, to my knowledge, not been described before, and most previously published observations of prepupal behaviour relate to captive larvae ; moreover, the pupa can seldom be discovered in its natural habitat.

Although in most cases it was not possible to observe the behaviour of the wild larva after it left the foodplant, I nevertheless succeeded in observing five wild pupations, and also discovered, soon or a longer time after pupation, about nine pupae *in situ* in the garden. Prepupal behaviour was, of course, also observed in my captive larvae, of which careful notes were made. The following interesting observations were thus noted :

Prepupal behaviour begins when the larva has stopped feeding and performed its final defecation, which in the case of Bagdad *machaon* is accompanied by a fairly copious emission of green fluid ; the behaviour consists of three successive stages :

(*a*) Walking, with intervals of resting with all feet in use ;

(*b*) constructing the silk carpet and pupal sling ;

(*c*) resting in the pupal sling attached by the anal hooks to the carpet, the feet not being of further use.

These three stages vary according to season. The first, for instance, is omitted entirely by larvae that have just aestivated and are subject to the great heat of early September ; as already stated (Section VII) these pupate on the foodplant near where the last mouthful was eaten. The first stage is abbreviated as the heat increases, for it was noted that pupation took place nearer the foodplant in April and May than between November and March. One pupa in April, 1955 (hotter than April, 1954) was discovered a few inches above the ground on the stem of the foodplant itself ; in this case the distance walked had not amounted to more than 12 inches, or, if the larvae forming it had perhaps come from another rue bush, not more than a little over two yards. Not only is the first stage shortened to the point of elimination with increasing heat, but all three stages are longer in the cool weather, shorter in the hot. Table I illustrates this in detail. Only the first stage can be entirely dispensed with ; the second and third are, of course, necessary and vital for all larvae, though they may be passed in a shorter or longer time. Consequently the interval between cessation of feeding and pupation may be as long as eight or nine days (in winter), or as short as one day (in summer). (In Table I, *see* Z7 and YY for the maximum, Q and S for the minimum, pre-pupal period.)

The selected pupal site also differs according to season. Not only is it further away from the foodplant in winter (as is natural since the walking stage lasts longer) but it is also more exposed, being then often placed high up on the south side of trees where they receive constant sunlight, not to mention occasional rain. In the winter of 1957, however, two newly formed pupae were found very low down in sunny places several yards from their foodplant. Summer pupae tend to be concealed amidst foliage where little or no sun falls on them. During more than one winter, larvae were observed climbing and later pupating on the trunks of palm trees at a distance of between seven and 11 metres from the foodplant. Pupation took place at heights of between one and three metres on these trees. The southern side was invariably chosen. Between April and October such pupal sites were never chosen. Some instinct thus appears to operate by which the pupa receives the moderate heat of winter but avoids the extreme heat of summer. Larvae and pupae were never seen by me on walls ; this was remarkable as walls surrounded the rue plot on two sides. However, a friend reported having once seen a pupa on the wall of his house. One of the two 1957 winter pupae which were found low down had, in fact, been formed on the southward-facing side of a loose brick lying on a flower-bed. To conclude, a vegetable substratum for pupation is preferred and in nearly all cases selected, when available.

X. The Pupa

(1) *Coloration*

The pupae were either green or brownish. The green forms were bright green with yellow dorsal tubercles ; the brown forms were variable.

The green forms were invariably those formed on the foodplant or on other flowers or amongst other foliage. The brown forms were those formed on the tree trunks and the brick, or formed in captivity on the wood, cardboard or gauze of cages.

(2) *Pupal Period and Diapause*

The pupal period varies more than any other stage, the minimum period observed being six days and the maximum 177 days. Nevertheless pupae not undergoing diapause spend a more uniform period before hatching, varying slightly according to the season, *i.e.* probably temperature. It is therefore best to treat the subject in two parts, the first dealing with pupae not undergoing diapause, the second dealing with aestivating or hibernating pupae.

First generation larvae produce pupae that never undergo diapause but which develop rapidly to produce second generation adults. Pupae of succeeding generations may develop quickly or may go into diapause. Prolonged experiments would be necessary to establish whether this division of pupae of the second generation into a quick-developing group and into one with diapause is genetically controlled, as seems likely. It has not been possible to undertake such experiments. Quick development of pupae also occurs after larval diapause, and in such cases, as far as my observations go, is the invariable rule ; the same individual that has undergone larval diapause never undergoes pupal diapause.

In quick-developing pupae the absolute minimum period observed was that of September, 1954, after larval aestivation ; these pupae emerged after six or seven days and were on the wing roughly at the same time as, or slightly before, the butterflies hatching from over-summering pupae. In quick-developing pupae of first generation larvae, I observed a period of about 11 days (*see* individuals L, M, P in Table I) and this corresponds to pupal periods of 9 to 14 days observed in May–June in the Dyala region by Peile.

In winter, especially mild winters such as 1954–55, some pupae spend too short a period in that stage for it to be considered a diapause at all (*see* J and ZZ in Table I). A period of only 16 days (J) can hardly be considered a diapause, and the next shortest period observed, namely 28 days (ZZ), might perhaps similarly be considered not to be hibernation. It is probably significant that both of these cases were late winter larvae, while the long hibernation periods in pupae were from October larvae. Can one go so far as to say that where larval growth has been retarded by the cold to a marked extent, the effect is somewhat similar to that of the larval diapause, namely a reduction in length, if not the actual elimination of, the pupal diapause? It would seem, in any case, that the later the pupation, the shorter the pupal period. This is so from the winter evidence, and may be so in summer (though less evidence is available for this). So remarkable is the irregularity in the pupal period of *machaon* that it can probably best be explained as jointly controlled by hereditary and climatic factors.

I took advantage of my 1955 summer absence to experiment on some already aestivating pupae by giving them a change of climate, and the results appear to indicate that the summer diapause can be shortened in this way. In the exceptionally early season of 1955 pupal aestivation was observed to begin in May and might have been expected to last 130 days, *i.e.* a month longer than the pupal diapause observed in 1954, had the pupae been kept in Bagdad. Of five May 1955 pupae, two began to develop quickly and showed wing coloration before succumbing to parasites; the other three, all healthy, began a diapause, remaining pale in colour, but on 14th June, on leaving Bagdad I took them with me and reached England on 23rd June. In these abnormal conditions their diapause was shortened, the period being 40–50 days (*see* R, T, and U in Table I); this seems to indicate that the summer diapause of the pupa ends and the adult hatches one to two weeks after the cessation of extreme heat. The coolness of my study in Bagdad was not such as to prevent or abridge the diapause of the individual 4V in 1954, but the coolness of the English summer effectively shortened the diapause of R, T and U. The critical temperature is probably between 70° and 80° F., but of course the data from which this is inferred cannot be regarded as a controlled experiment.

Fewer pupae were observed in the summer diapause than in the winter, and caution is therefore necessary in comparing the two, but from the data it appears that the dates of emergence after aestivation in normal Bagdad conditions are more regular than those after hibernation. On the other hand, October oviposition dates suggest that, unless females are long-lived, not all aestivating pupae hatch in September. The maximum pupal aestivation period observed was that of 1954, 100 days; the maximum pupal hibernation period was that of 1956–57, 177 days. The latter is little more than half as long as that of the single-brooded races of *machaon*, e.g. subsp. *alpica* Verity (as observed and reported in Warren, 1951), which varies between 259 and 301 days. In England the maximum pupal period can evidently be occasionally more than 365 days (though never, as far as I am aware, is there a double overwintering), for some pupae from Wicken formed in captivity in summer 1934, hatched in early June, 1935, and (two) on 18th and 24th, July, 1935 (according to G. E. L. Manley, 1935).

To conclude, the pupae in Bagdad may develop quickly or may undergo diapause; but since these periods of diapause occur twice a year, for summer and winter extremes, they last less long than those in more northerly races where only hibernation occurs, and they do not exceed 180 days; the minimum length of the quick developing period is six days.

XI The Imago

(1) *Phenology*

Since death in a wild state was not observed, the imaginal period could not be ascertained exactly. Adults probably live not more than seven days after hatching; they are evidently incapable of diapause. The complete disappearance of the imago between mid-November and mid-March (in a normal year) and again between mid-July and the second part of September is very striking and in contrast with the phenology of other butterflies in the same habitat. As has been said, the variable pupal period leads to the appearance

of imagines spread over several weeks, and, were it not for the evident inhibition of pupal emergences between July and September and again between November and February, generations would overlap promiscuously throughout the year. As a result of these checks a rather rough and imperfect synchronisation of emergences is produced twice a year. The number of annual generations is not as clear as in certain other species. *P. machaon* is evidently a potentially multivoltine species, and its Bagdad colony has between three and five generations a year. It is impossible to be more exact about the number in view of the observed facts. The length of the cycle from egg to egg in the most favourable circumstances and in the absence of any diapause, is about 51 days. Even in a normal year and allowing for a summer diapause, there would at this rate be time for five generations between March and November, *i.e.* (1) March, (2) mid-May, (3) July, (4) mid-September and (5) early November. But the quick development of June and October pupae is only partial; consequently the third brood hatches partly before and partly after the midsummer diapause while the last brood of butterflies most probably has a similarly split emergence, *i.e.* partly before and partly after the winter diapause. Observations of flying adults seem, in fact, to indicate five annual emergences, but whether the individual seen has hatched from a quick-developing pupa or after a diapause cannot be ascertained in such observations, still less whether its parents so hatched. Five generations in a single year have not been reared experimentally. It is even possible that there are, in fact, only three generations of surviving stock and that the descendants of quick-developing individuals come to grief or are never born. This might occur through lack of sexual development in quick-hatching pupae in midsummer; at least, although July butterflies were seen flying in 1954, no resulting ova or young larvae were observed. The butterflies seen may, of course, have oviposited elsewhere and for some reason or chance failed to do so in my garden; but this seems improbable since ova or young larvae were seen shortly after all other visits observed in every month except July. It seems more probable that the July butterflies were incapable of laying. The disadvantage, in evolution, of quick development, assuming this explanation to be true, would nevertheless not cause the quick-developing strain to be eliminated because it is not so disadvantageous at other times of the year and in other generations. A second way in which descendants of quick-developing individuals may come to grief will be discussed under predation (Section XII).

For the above reasons one must be content with saying that the Bagdad colony of *machaon* has at least three and perhaps five annual generations. In southern Italy and some other Mediterranean countries, where the season, though similar, is shorter than in Bagdad, Verity (1947) states that there are three annual broods with a partial fourth of *machaon* subsp. *sphyrus* Hübn. Probably the phenology of the Bagdad colony of subsp. *centralis* is similar to that of the North African subsp. *saharae* Ob. which Eller says has four generations, on what authority is not clear. But from Verity's remarks, from Manley's observations in England (Manley, 1935), and the Bagdad and Shiraz phenology, partial quick pupal development, with diapause as the alternative taken by the other part of the brood, appears a regular characteristic of the species and not a peculiarity of one population or subspecies alone. Probably, therefore, in all populations occurring where there is a long summer, closer observation

will prove that it is as difficult to give the precise number of annual generations as with the Bagdad colony.

(2) *Facies*

The imago varies seasonally both in coloration and wing-shape.

In colouring the black pigmentation of the uppersides of both wings and of the body varies in intensity and extent; one may distinguish four gradations:

(*a*) The subcostal space is darkened and the thorax and abdomen, viewed from above, appear dark; this form is the nearest to the British native form (Pl. I, fig. 1).

(*b*) The subcostal space is pale, and on the thorax and abdomen, viewed from above, a yellow border on either side of the black central stripe is clearly visible.

(*c*) The black central stripe on the thorax and abdomen is still narrower and on the wings the black pigmentation, especially the black cloud near the anal margin of the hind wing, is reduced.

(*d*) The black central stripe has disappeared from up to six of the abdominal segments (Pl. I, fig. 2). (This form, in the North African subspecies, has been named *xanthosoma* (Turati).

It may be added that the wings are shorter and rounder in (*a*), more elongate and falcate in (*b*), (*c*) and (*d*).

The greatest degree of black pigmentation occurs in the first generation in the Bagdad colony after a normally cold winter, but in some years even after a cold winter form (*b*) rather than form (*a*) is usual in the first generation. The least degree occurs in midsummer. A given brood may not have the same facies in different years; for example, the 1954 first generation was form (*a*) (Pl. I, fig. 1) but in 1955 and 1957 the first generation were form (*b*). Later broods vary similarly. In 1954 June and October butterflies were form (*b*) and July and September butterflies were form (*d*); in 1955, the third generation, appearing in May, was form (*c*). The aestivating pupae, taken in 1955 to England, and from which, if left in Bagdad, form (*d*) was to be expected, in fact produced forms (*b*) and (*c*), which are actually the commonest in Bagdad.

Variation of ground colour also occurs. Most examples are yellow when fresh but a minority have a whitish ground colour. Of those bred in 1954–55, 19 were yellow and one only was whitish.

The adult form, therefore, at least in the degree of black pigmentation, exhibits variation evidently due to environmental influences, especially temperature. The same, it was shown, was the case with the black pigmentation and other coloration in the larva (*see* Section IX (1) above). It may, therefore, be asked whether there is a linkage between melanism in the larva and adult facies in individuals, *i.e.* whether perhaps the excess of pigment in the larval form *nigricans* is actually the same pigment responsible for the blacker appearance of form (*a*). The answer to such a question must evidently await careful dissections of larvae and pupae, but meanwhile the following relevant facts may be noted.

Firstly, the black pigment seen in *nigricans* larvae is lost by the organism at pupation, when the skin, in which it is deposited, is sloughed off. It may

be that somewhere in the pupal interior more pigment is stored; the pupal integument of brown pupae shows a slight capacity to vary between light brown and brown with darker markings, but such variation does not appear on the integument of green pupae. Brown pupae do, in fact, tend to have more dark markings in winter than in summer, but the tendency is less than in the larva. The pigment seen in these pupal integuments is likewise lost by the organism at emergence, when the adult breaks out of it.

Secondly, whether or not the black pigmentation of the adult is the result of something that has happened to the larva, it cannot be denied that what happens to the pupa seems to modify the effect. Pupae from *albicans* larvae of May, 1955, when transferred to a cooler country, produced forms (*b*) and (*c*) instead of (*d*). Of those performing the normal cycle in Bagdad, in 1954, adults of form (*d*) resulted both from *albicans* larvae and from normally coloured larvae. Similarly first generation adults are not composed entirely of individuals that as larvae were form *nigricans*, some being from normal larvae that pupated earlier in the previous winter. It may also be added that the larval form *nigricans* appeared both in the normally cold and in the mild winter months, but the adult form (*a*) only appeared in the first generation after a cold winter, and was rarer than the larval dark form.

The first instar of the larva has the most complete black pigmentation. It would appear that fresh deposits of black pigment can be made throughout the life of the individual at every metamorphosis, but with diminishing effect; great heat and brilliant light reduce the effect more quickly than cooler, duller and more humid conditions. The degree of black pigmentation in the adult appears to depend on the external conditions to which first the larva and later the pupa are subjected. The conditions experienced by the pupa may partly counteract an effect due to larval experiences. In the Bagdad colony the degree of black pigmentation appears, from the above observations, not to be genetically produced. The whitish adult form, on the other hand, where the upperside wing colour is not yellow, may well be so produced.

XII. Predators

The Bagdad colony of *machaon* at first appeared rather immune to predation but later proved to suffer from a varied assortment of enemies. Sparrows, large predatory wasps, spiders, chalcid wasps and dipterous parasites were observed. No ichneumonid parasite was seen, which was remarkable in view of the existence in the garden of an ichneumonid preying on other lepidopterous larvae, *e.g.* on *Carcharodus alceae* subsp. *insolatrix* LeCerf, and the fact that in Europe *machaon* has a well-known ichneumonid enemy, *Trogus lapidator*. What was also remarkable was the seasonal incidence of predation, and the comparative immunity of winter-feeding larvae and pupae.

The sparrows were only observed to attack the larvae in April 1955. They had nestlings at the time; moreover, the *machaon* larvae of the first generation were in this month and year unusually numerous and conspicuous; there were at least 40 full-grown larvae on the dill plot and at least 80 on the five large rue bushes. This exceptional concentration was due to a damaged female butterfly having remained in the garden in March for several days, its flight having been weakened, and plenty of the requisite foodplant being available. Once a pair of sparrows began preying on the larvae others imitated them,

pecking and finally carrying off larva after larva. In two or three days all were gone except five or six, which I rescued in time and took indoors. The only other larvae of this brood to escape were those that reached maturity a week before the others and which had pupated before the attacks began. But most of these pupae were killed by Chalcids.

The Chalcid wasp, whose identity Mr. Perkins of the British Museum has kindly confirmed to be the well-known *Pteromalus puparum* L., was principally active in April and May. Several *machaon* first generation pupae were observed on flower stems in the garden in April 1955, with a single female of *P. puparum* sitting on them ; the wasp remained usually for 24 hours or more. One such pupa was taken and 335 Chalcids emerged from it after a life-cycle of 15 days, and a smaller number emerged after an aestivation of several months. During these 15 days the pupa lost its natural bright green hue and gradually became a leaden green. The non-aestivating parasite adults all emerged at one time, about 5 p.m. on 25th April, through a single hole bored in the wing-case of the pupa (but one or two dead pupae were later seen in the garden with two holes in the wing-case). The male wasps outnumbered the females by about 50 and were much smaller. In the middle of May 1955 and again in October 1956, when the later generation larvae were full grown, single females of probably the same species of Chalcid were observed sitting on the back of the larvae or walking on the stems and leaves close to them. In order to see whether oviposition had already taken place, six such larvae were taken (individuals Q, R, S, T, U and VV in Table I) into captivity. No Chalcids emerged from the resulting pupae, of which two died and four produced healthy adults. The two that died showed wing colouring before the rest of the body blackened. From one of them a dipterous parasite emerged, and promptly formed a small pupal capsule, which failed to hatch. The death of the second pupa is unexplained, since the adult appeared fully developed within the pupa-case when examined. From these observations one concludes that the Chalcid females were waiting for the larvae to pupate before ovipositing. No specimens of the May and October Chalcids were examined and it was assumed that they were the same species as in April. Since diapause was observed in *P. puparum* in captivity, this assumption is probably correct. The autumnal and winter pupae were apparently unaffected by these Chalcids, which presumably die off in October before most of the larvae pupate ; but doubtless some early pupae in October are victimised, though this was not observed. Predation by both sparrows and Chalcids, therefore, was seasonal and greatest in April. From May to October, when the larvae were less numerous and feeding lower down on the bushes of rue, the sparrows did not appear to notice them and no attacks like those in April were seen. Similarly in October to February, although larvae fed higher on the foodplant, sparrows were not observed to attack them, though the larvae were quite numerous in December 1954.

In the hottest season, the small larvae were ruthlessly decimated by predators, not all of which could be identified. In June 1955, young third generation larvae were preyed on either a few days after hatching or not later than the third instar. In mid June I was unable to find a single survivor on the rue bushes (of which the garden now contained 5 large and 33 small plants). The orange-coloured wasp *Polistes hebraeus* Fabr. was observed carrying young first instar larvae from rue leaves ; it was seen constantly hunting among the

rue plants. Spiders were also apparently actively preying on the young larvae at this season, for three or four mangled corpses of third instar larvae were found on the rue leaves. Attacks by spiders were not actually observed but the rue bush where these traces were found was inhabited by couples of a species of green cryptically-shaped spider. In early October, 1954, the corpses of small larvae were also noted, close examination of one of which showed a gaping wound on the back ; the corpse had been sucked dry. Victims of this kind of attack were not observed in the cooler weather, *i.e.* before June or after mid-October, but during the hot season the joint efforts of *P. hebraeus* and the other predator accounted for almost 100 per cent. of small larvae. The survival value of the longest possible aestivation in these circumstances is evident, and may be one of the factors that have caused it to develop in some univoltine species to such a marked extent.

To sum up, there was virtually no predation between October and March, but it was intense from April till mid-October.

XIII. Unsolved Problems

It is hoped that future observers in Bagdad will try to solve the following three problems, especially the first :

(1) Exactly where do aestivating and hibernating larvae spend the diapause? Only when this is directly observed can the estimates made in this paper of the larval period, etc., be confirmed or corrected.

(2) Do the occasional July butterflies oviposit? If not, is it because females are not sexually developed?

(3) If several generations could be bred entirely in captivity and notes kept of the phenology of more than one lineage, as well as the colouring of larvae and adults, the part played by heredity and environment respectively in these phenomena in Bagdad will perhaps be further illuminated.

XIV. Summary

The environment and foodplants of the Bagdad colony of *Papilio machaon* L., which is part of the so-called subsp. *centralis* Stgr., are described. It derives from the Zagros and Dyala populations but differs in being dependent on cultivated plants, principally *Ruta graveolens* L. The density of the adult population is low. The egg stage is short and hardly varies. A month by month account of its annual life-cycle, with variations due to the weather of four different years, is given. If there is no diapause the larval period varies from 30 to about 60 days, but a larval diapause in the last instar sometimes occurs. The diapause is more usual in the pupal stage, but at certain seasons does not occur at all in an individual life-cycle. The black pigmentation of the larva is reduced if the heat is great and the light intense, but promoted by cooler weather, humidity and shade. The facies of the adult seems to respond similarly to external conditions. The larva's feeding and prepupal behaviour, and selection of pupal sites at different seasons are described. This behaviour also varies in response to the weather. Pupae are green when placed among foliage, brown when on wood or other non-verdant substrata. The pupal period varies in length between 6 and 177 days, and the longer periods are due to diapause, tiding the pupa over midsummer or winter. The third generation adult

may emerge before midsummer or in September after aestivation, the brood dividing. The final generation is also presumed to be partial, some pupae probably hatching in November, others certainly overwintering. Autumnal larvae grow rather slowly and at a less regular rate than summer larvae and many do not pupate until early the following year. There appear to be five emergences but there are probably only three or four annual generations. The various predators are described; one is the Chalcid *Pteromalus puparum* L., the females of which sit on mature larvae of *P. machaon* but do not oviposit before pupation. Predation varies seasonally, being severe in summer.

XV. References

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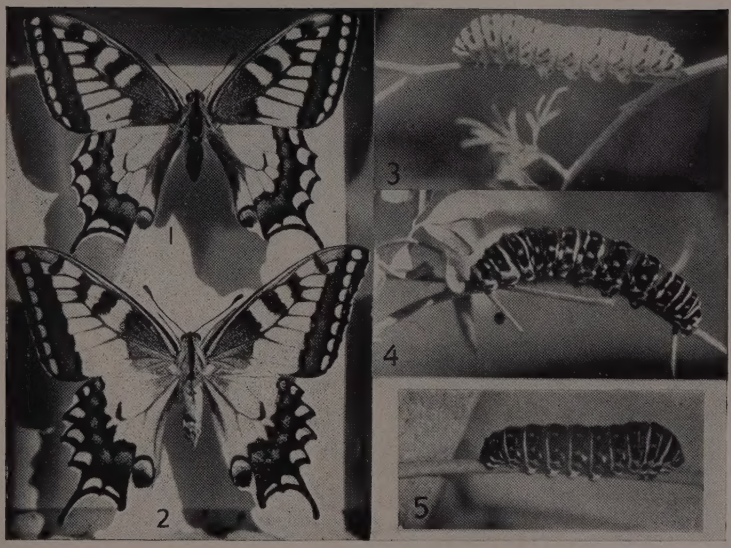

Fig. 1.—*Papilio machaon* L. ssp. *centralis* Stgr. : first generation, Bagdad.

Fig. 2.—The same : third generation, Bagdad.

Figs. 3–5.—Larvae of above : (3) f. *albicans*, May, 1955, on dill ; (4) f. *nigricans*, January, 1955, on rue ; (5) extreme f. *nigricans*, January, 1955, on rue.

E. P. Wiltshire.

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